

A NEW PALAEOONTOLOGICAL TECHNIQUE DESCRIBING TEMPORAL SHAPE VARIATION IN MIOCENE BIVALVES

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ABSTRACT. Principal components quantitative shape analysis (PC shape analysis) is demonstrated to be a rapid and effective palaeontological morphometric technique for quantifying shape. It allows easy interpretation, as morphology can be reconstructed from PC scores. Results of PC shape analysis have revealed that temporal patterns of shape variation in four Chesapeake Group (Miocene) taxa from Maryland are not congruent. Whilst there was a significant monotonic trend towards more disc-shaped valves in *Dosinia acetabulum*, there was no significant temporal trend in *Lucina (Stewartia) anodonta* valve shape. Whilst the evolutionary tempo in an *Anadara* lineage was more consistent with punctuated equilibrium, with interspecific changes controlling ultimate shape transformation and reversing intraspecific trends, the *Astarte* lineage had an evolutionary tempo not inconsistent with phyletic gradualism, where intraspecific trends were generally preserved during speciation.

PRESENTLY, no universal method for measuring shape exists. Commonly, morphological techniques utilize measured distances between homologous landmarks as shape variables (reviewed in Bookstein *et al.* 1985). However, if there is a paucity of distinct homologous landmarks (e.g. with simple invertebrates) shape information will be limited. The development of automated image analyzers has led to the creation of better techniques for describing simple invertebrate shape by making use of a nearly continuous representation of an organism's outline. Whilst the outline may not include all critical morphological features, our perception of differences in shape is based largely upon outlines (Scott 1980). Like Fourier (Schwarz and Shane 1969; Ehrlich and Weinberg 1970) and Eigenshape analysis (Lohmann 1983), the PC shape technique (Parks 1983, 1987) has been developed to process the large data sets generated by image analyzers.

The major objective of this study was to develop the PC shape technique as a palaeontological tool for describing temporal variation in bivalve morphology. Miocene bivalve genera from southern Maryland were selected because the stratigraphy and palaeoecology of the Chesapeake Group and the taxonomy, taphonomy and palaeoecology of the genera have been studied extensively. The results are compared with earlier studies which describe evolutionary tempos of the same Chesapeake Group genera from Maryland.

MATERIALS AND METHODS

Study area and bivalve taxonomy

Temporal variation in shape was characterized for eight Early to Late Miocene bivalve species, comprising *Dosinia acetabulum* (Conrad), *Lucina (Stewartia) anodonta* Say, *Anadara subrostrata* (Conrad), *A. staminea* (Say), *A. idonea* (Conrad), *Astarte cuneiformis* Conrad, *A. thisphila* Glenn and *A. perplana* Conrad (Table 1, Text-fig. 1). In a written communication to Kelley (1983a), Blackwelder recognized the congeners of *Anadara* and *Astarte* as being part of lineages with direct ancestor/descendant relationships. Taxonomies are based upon Glenn (1904) with revisions by Vokes (1957), Moore (1969) and Bretsky (1976).

TABLE 1. Number of specimens sampled in each 'zone'.

Taxon	'Zone'						
	10	14	16	17	19	22	24
<i>Anadara</i> sp.							
<i>A. subrostrata</i> (Conrad)	36						
<i>A. staminea</i> (Say)			16	17	37		
<i>A. idonea</i> (Conrad)						60	96
<i>Astarte</i> sp.							
<i>A. cuneiformis</i> Conrad	45	3					
<i>A. thisphila</i> Glenn			7	36	3		
<i>A. perplana</i> Conrad							32
<i>Dosinia acetabulum</i> (Conrad)			10	22	6	41	42
<i>Lucina</i> (<i>Stewartia</i>) <i>anodonta</i> Say	39			37	12	9	69

Species were identified and traced in the field in order to preclude the loss of samples through breakage during transport. Whole shells only were collected, and thus the study is biased towards better preserved bivalves. Furthermore, adult specimens within a narrow size range were sampled to limit ontogenetic effects.

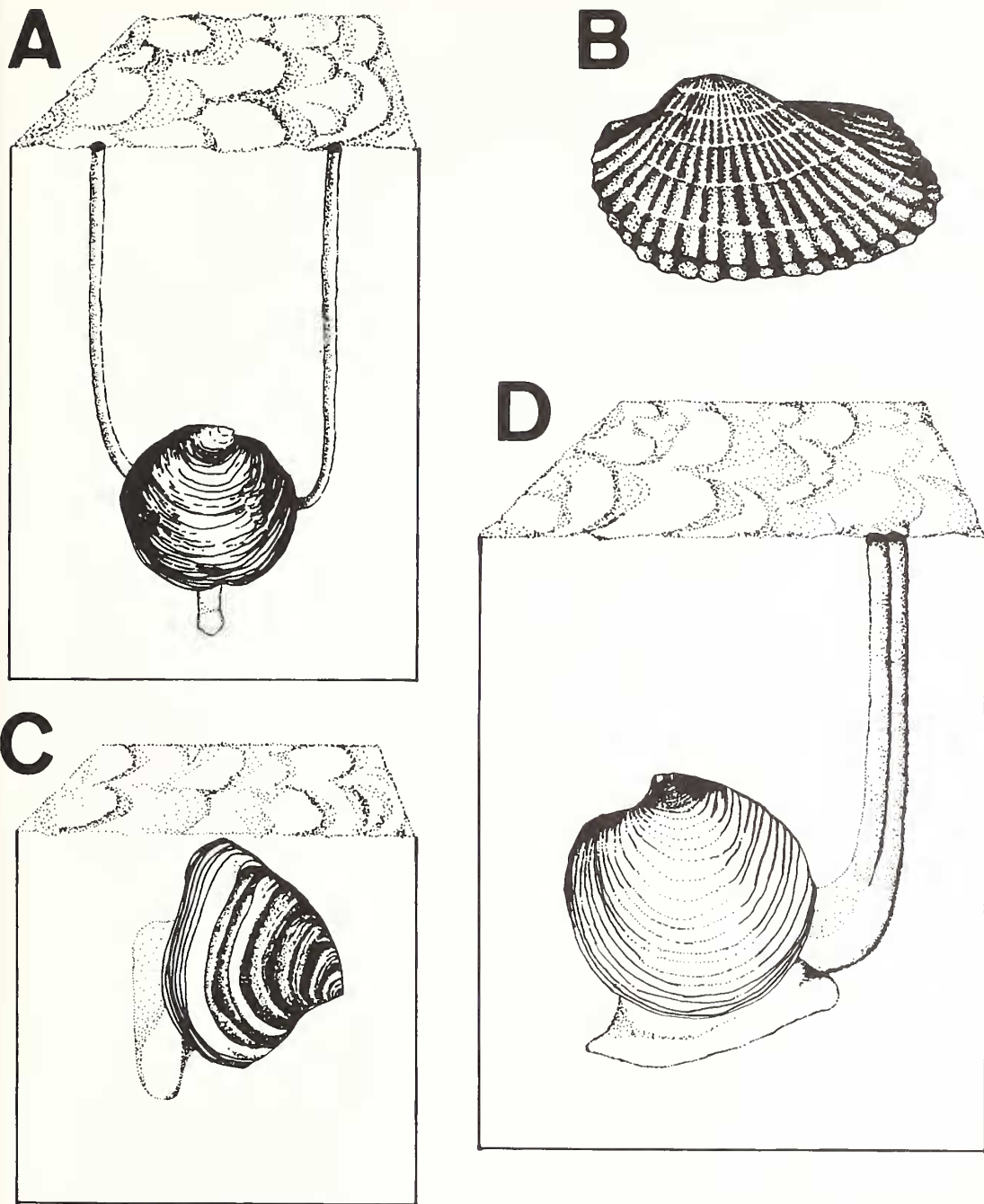
Fossils were collected from fifteen exposures located principally along the western shore of Chesapeake Bay (Text-fig. 2). The strata are part of the Chesapeake Group which is nearly continuously exposed for approximately 60 km, trending north-south, and coinciding roughly with the southerly dip direction of the unconsolidated siliciclastics. The Chesapeake Group in southern Maryland has been divided into three formations, designated the Calvert, Choptank and St Mary's formations (Shattuck 1904; Text-fig. 3). Shattuck (1904) subdivided the formations into twenty-four 'zones' based upon lithology and major shell beds. Difficulties in recognizing formation contacts (Dryden 1930; Gernant 1970; Blackwelder and Ward 1976) and the disputed assumption that all of the 'zones' are laterally continuous and synchronous has led to controversy surrounding the stratigraphical relationships and nomenclature. However, it was not an objective of this study to tackle stratigraphical problems within the Chesapeake Group and therefore, for the purpose of this study, Kidwell's (1988, 1989) classification scheme has been adopted (Text-fig. 3).

The Miocene of southern Maryland records a period of regression during which marine, paralic and non-marine sediments were deposited within the Salisbury embayment (Gibson 1962; Gernant 1970; Kidwell 1988). The Salisbury embayment (which is an extension of the Baltimore Canyon trough) is a structural basin the depth and boundaries of which have varied with changes in tectonic and eustatic controlling factors (Newell and Rader 1982). Basin margin disconformities bracket ten transgressive-regressive cycles which commonly contain major shell beds at their base, representing condensed transgressive lag deposits (Kidwell 1984, 1986).

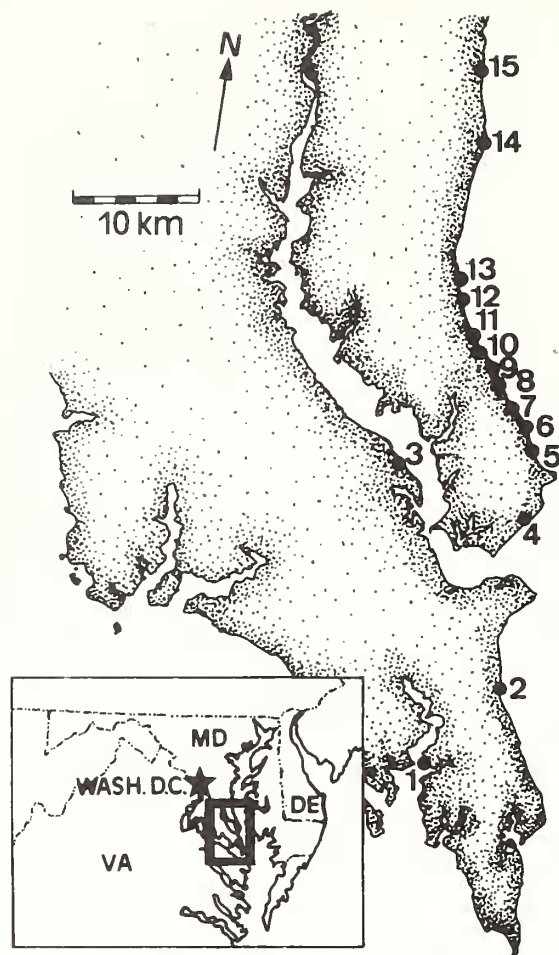
The PC shape technique

Fossil outlines were digitized using a Houston Hipad II digitizing tablet and stylus. Approximately 150–200 data points were recorded for each shell using FORTRAN77 program, DIGITIZE, written by Parks (1983, 1987). Operator error, determined by digitizing the same set of shapes twice, was 0.5 per cent.

Fossil outlines were rotated to a common orientation using one of two FORTRAN77 programs, BINPAXM or MODROT3, developed and written by Parks (1983, 1987). Elongate genera were rotated using BINPAXM which first calculated the principal eigenvector or axis of greatest length, according



TEXT-FIG. 1. A, inferred life position of *Lucina* (*Stewartia*) *anodonta* Say according to Bretsky (1976). B, *Anadara subrostrata* (Conrad). C, inferred life position of *Astarte thisphila* Glenn according to Stanley (1970). D, inferred life position of *Dosinia acetabulum* (Conrad) according to Gernant (1970).

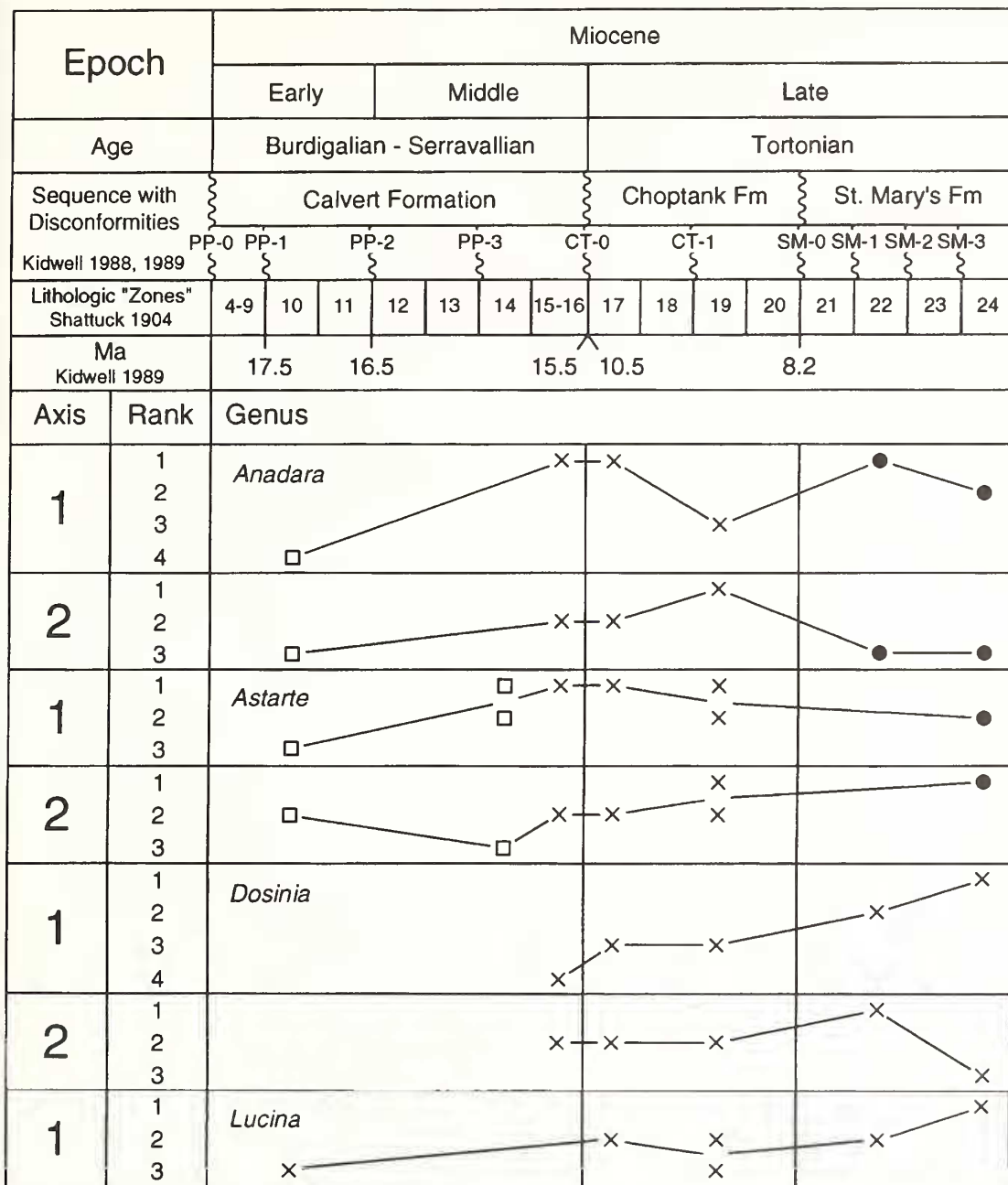


TEXT-FIG. 2. Map of the West Shore of Chesapeake Bay, Maryland with sampling localities: locality 1, Chancellor's Point; 2, Langley's Bluff; 3, Drumcliff; 4, Little Cove Point; 5, Calvert Cliffs State Park; 6, Camp Baybreeze; 7, Rocky Point; 8, Camp Conoy; 9, Flag Ponds Wildlife Reserve; 10, Calvert Beach; 11, Mataoka Cottages; 12, Kenwood Beach; 13, Governor Run Beach; 14, Plum Point; 15, Randle Cliffs Beach.

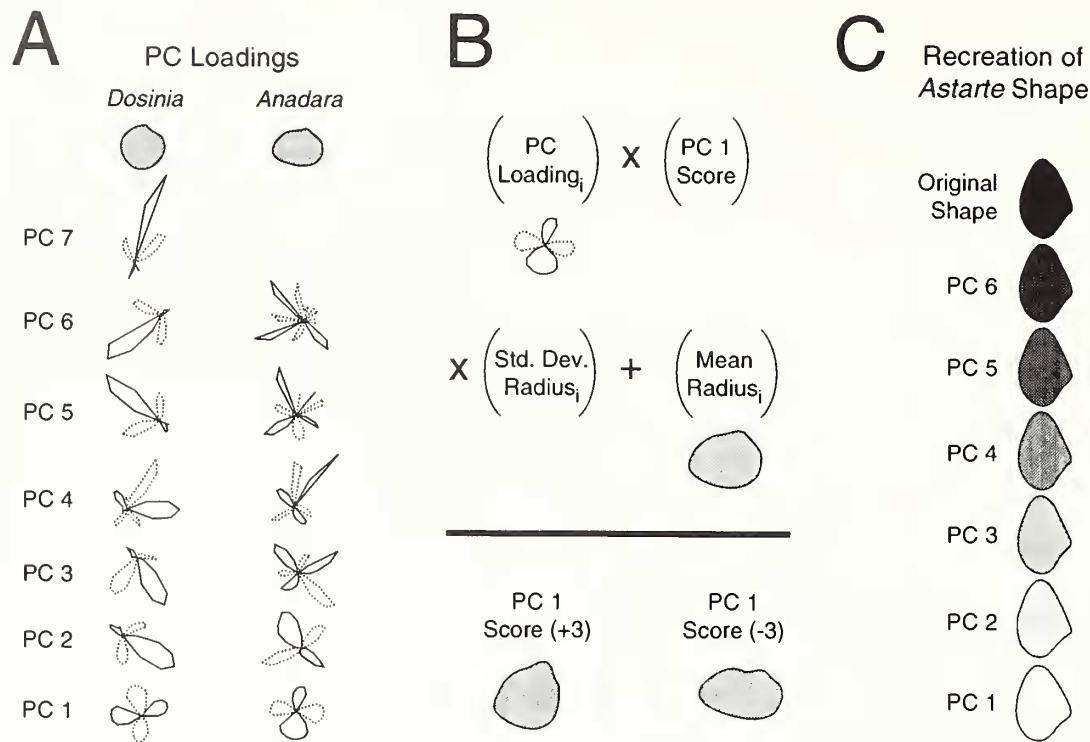
to the method of Tough and Miles (1983), and then positioned the principal axis in a horizontal orientation. This method worked well with elongate genera because the principal eigenvector was consistently orientated with respect to biological landmarks. However, with more rounded genera the principal axis was not consistently orientated. Thus the positioning of biological landmarks varied between specimens. In order to orientate consistently more rounded genera, MODROT3 was used because it rotated outlines to place the beak directly above the calculated centre-of-gravity.

After rotation, thirty-six radial lengths were calculated from the centre-of-gravity to thirty-six points interpolated around the margin at 10° intervals using a cubic curve fit procedure, with the first radial always connecting the tip of the umbo with the centre-of-gravity. The outlines were then rotated around the x and/or y axis according to a best least squares fit to an asymmetrical reference shape. In order to eliminate size effects the data were normalized by dividing an individual's radials by its mean radial length.

A χ^2 test was performed to verify that every variable (radial length) within a data set fitted a normal distribution at the 0.05 significance level. Data matrices containing thirty-six radial lengths of congeners were reduced by principal components analysis (using FORTRAN77 program BMDP4M; Frane *et al.* 1985) to six to seven principal components (PC) each accounting for a variance greater than or equal to one (Table 2). The PCs cumulatively accounted for approximately 90 per cent. of total shape variation which was found to describe shape adequately (Text-fig. 4c).



TEXT-FIG. 3. Stratigraphy and age of Chesapeake Group sequence and homogeneous groups of taxa computed by multiple range analysis using canonical variate 1 (Axis 1) and 2 (Axis 2) scores; in *Anadara* groups – square is *A. subrostrata*, x is *A. staminea* and dot is *A. idonea*; in *Astarte* groups – square is *A. cuneiformis*, x is *A. thisphila* and dot is *A. perplana*.



TEXT-FIG. 4. A, plots of *Dosinia acetabulum* and *Anadara* PC loadings. B, equation used to recreate shape from PC scores and loadings; reconstruction of two specimens of *Anadara* using PC scores +3 and -3. C, reconstruction of an *Astarte* fossil shape by the cumulative addition of PC 1 through PC 6 to average shape.

TABLE 2. Variance explained (expl.) and cumulative per cent. of variance (cum.%) for each PC having a variance ≥ 1 .

Genus:	<i>Anadara</i>		<i>Astarte</i>		<i>Dosinia</i>		<i>Lucina</i>	
Variance:	Expl.	Cum.%	Expl.	Cum.%	Expl.	Cum.%	Expl.	Cum.%
PC								
1	19.23	53	18.96	53	14.87	41	13.31	37
2	5.53	69	5.39	68	5.65	57	9.29	63
3	3.12	77	4.59	80	4.24	69	3.73	73
4	1.96	83	1.57	85	2.89	77	2.52	80
5	1.43	87	1.48	89	2.07	83	1.58	85
6	1.19	90	1.15	92	1.45	87	1.33	88
7					1.08	90		

Analysis of evolutionary trends

PC scores for each individual were estimated by post-multiplying its standardized set of thirty-six radial lengths by the matrix of PC loadings. The scores essentially represent the amount of a PC that is contained in a shape. As PC 1 contributed the most to shape variation (Table 2), PC 1 score

frequency histograms at each stratigraphical level were plotted to reveal evolutionary trends in a single species or lineage. The histograms were presented with reconstructed end member shapes to facilitate the interpretation of morphological trends. Within a single lineage, if the direction of an intraspecific shape trend was retained with the transformation of that species into the next, phyletic gradualism was inferred. Morphological change within a lineage would also have to be equally influenced by inter- and intraspecific shape trends. In contrast, if interspecific trends varied markedly in direction from associated intraspecific changes, the punctuational model was implied. In addition, interspecific changes should control the ultimate shape transformation of a lineage. Kruskal-Wallis one-way analysis by ranks was used to determine whether there was a significant difference between PC 1 scores of stratigraphical populations within a genus.

Morphological differences between stratigraphical populations of a genus were quantified using estimated PC scores as input variables in multi-group discriminant analysis (using FORTRAN77 program BMDP7M; Jennrich and Sampson 1985). Mahalanobis distances were computed between stratigraphical population means and between each specimen and its corresponding stratigraphical population centroid. The percentage of individuals in each taxon correctly and incorrectly classified according to 'zones' of occurrence was reported as was the percentage of individuals in each lineage correctly and incorrectly classified according to species. Successful classification of stratigraphical populations and the placement of a high percentage of individuals into stratigraphically proximal 'zones' implied a gradual change, where mixing of individuals from proximal 'zones' was due to the existence of intermediate morphologies.

Canonical variate 1 mean scores of stratigraphical populations, calculated by discriminant analysis, were plotted and the morphological meaning of trends was represented by the shape of individuals with canonical scores most closely approximating group means. Group centroids were used instead of individual canonical variate scores to make trends more easily recognizable. A non-parametric rank correlation technique was used to search through group centroids of all of the canonical variates of a taxa to find significant monotonic trends. Spearman's rank correlation coefficient, *C*, was calculated to quantify the relationship between temporal order and the order of group centroids along a canonical variate axis. Multiple range tests (STATGRAPHICS software; Statistical Graphics Corporation 1988) were performed using canonical variate 1 and 2 mean scores of stratigraphical populations of congeners. The statistical technique employed least significant difference (LSD) of means at the 95 per cent. confidence level in order to determine the presence of homogeneous stratigraphical populations. The homogeneous groups were plotted against time and associated stratigraphical level in order to show the maximum time interval in which a significant change in canonical variate 1 and 2 score means and, thus, shape occurred.

COMPARISON WITH ALTERNATIVE METHODS OF SHAPE ANALYSIS

The need to quantify shape was recognized by Thompson (1915), who used cartesian coordinates to describe the shape of one organism as the distortion of another. Benson (1981) more recently developed a morphometric technique using a similar approach. However, rather than explaining shape change in terms of homogeneous plane strain, as in Thompson's model, he examined the differential deformation of geometrical representations of homologous parts in relation to overall form. Both methods rely on the recognition of homologous points to compute morphological changes. Point to point measurements have been used widely in biometric studies, probably for reasons of instrumental limitations and past precedents, rather than theoretical considerations (Scott 1980). The development of alternative morphometric techniques to process outline information (e.g. Fourier, Eigenshape and PC shape analysis) has proven to be useful when describing simple invertebrate shape where there are few homologous points along the periphery.

Both Eigenshape (Lohmann 1983) and PC shape analysis use multivariate statistics to reduce orientated fossil outline information to fewer principal components. One difference between PC shape and Eigenshape analysis is the method of representation of an organism's outline. While PC

shape analysis uses equiangular radial lengths about an organism's calculated centre of gravity, Eigenshape analysis uses net angular changes in direction at each step around a perimeter (preferred technique where there are re-entrants along a shape's periphery). Another difference between PC shape and Eigenshape analysis is the calculation of principal components based upon covariances among shapes versus correlations among shapes. Whereas the first principal component in PC shape analysis describes maximum shape variation among organisms, the first Eigenshape describes the average shape of a group of organisms. More recently, users of Eigenshape analysis have started to use covariances among shapes in principal components analysis (e.g. Schweitzer and Lohmann 1990). A strength of multivariate shape methods, such as Eigenshape and PC shape analysis, is that the first k basis vectors (principal components) account for more variation in a data set than the first k basis vectors of other methods, such as the Fourier technique, whose basis vectors are the Fourier harmonics.

The Fourier method characterizes shape using a harmonic Fourier series of the expansion of the radius as a function of the angle about the centre of gravity. The harmonics are computed from:

$$R(\theta) = A_0 + \sum_{n=1}^{\infty} A_n \cos(n\theta - \Phi_n),$$

where R is a radius vector measured from a shape's centre of gravity to a point on the periphery in the polar direction θ , A_0 is the mean radius of the shape, A_n is the amplitude and ϕ_n is the phase angle of the n th term in the series.

Each Fourier harmonic represents a certain shape element, with the lower harmonics describing gross morphology such as elongation (2nd harmonic) and triangular shape (3rd harmonic), and the higher harmonics describing bumps on a shape such as scalloped edges due to ribbing. When the thirty-six radial loadings of each PC (generated by the PC shape technique) are plotted they resemble Fourier harmonic shapes (Text-fig. 4A). There are, however, some profound differences: (1) Fourier harmonics add nodes or loops with an increase in harmonic value while increasing PCs may retain the same number of loops but orientate them differently; thus, PC 1 and 2 might both describe elongation but be offset by 45°; (2) Fourier harmonics have symmetrical loops of equal size, while PC loadings form asymmetrical loops of various sizes.

The significance of the asymmetrical positive and negative loops becomes apparent when PC scores are combined with PC loadings to recreate a shape (Text-fig. 4B). A large negative PC 1 score combined with the PC 1 loadings of the *Anadara* genus creates an elongate shape with a larger length than height, whereas a large positive PC 1 score creates a rounder shape with a roughly equivalent length and height. PC 1 loadings in all of the genera consist of four loops orientated along x (anterior–posterior) and y (dorsal–ventral) axes of elongation, but the orientation of negative and positive loops in the round genera is offset by 90° of the elongate genera (Text-fig. 4A). Elongate species have negative loadings orientated along the anterior–posterior axis, while negative loadings of round species are orientated along the dorsal–ventral axis. Increasingly negative PC 1 scores will generate increasing shell length/height (L/H) ratios in elongate species and decreasing L/H ratios in round species.

PC 1 defines an elliptical component in all of the species. PC 2 also defines an elliptical component but at a different orientation to PC 1. PC 3 and 4 generally represent a triangular component at two different orientations and PC 5 and higher PCs represent more complex shapes. The relative contribution of each PC to shape is presented in Text-figure 4C, where, PC 1 was first added to the average shape of the *Astarte* genus according to the equation in Text-figure 4B, followed by the cumulative addition of increasing PCs. The importance of the contribution of PC 1 in recreating shape is demonstrated by the close approximation of the original morphology. PC 2 and 3 add further detectable shape modifications but are less important than PC 1. Shape modifications added by PC 4 and higher PCs are less discernible.

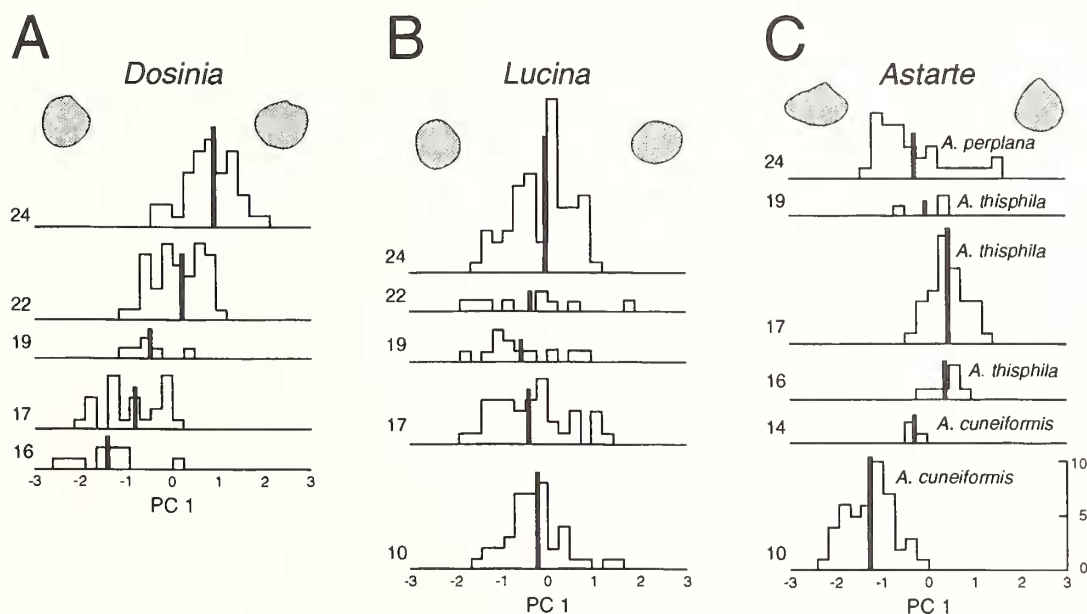
More PCs were required to account for approximately 90 per cent. of total shape variation in the more rounded genera, *Dosinia* and *Lucina*, because PC 1 accounted for less variation in shape than

in the elongate genera, *Anadara* and *Astarte* (Table 2). The greater contribution of PC 1 to the shape of elongate genera is due to the importance of variations in shell length versus height.

TEMPORAL TRENDS IN BIVALVE SHAPE

Dosinia acetabulum (Conrad)

PC 1 frequency histogram plots and the plot of canonical variate 1 group centroids show that valves evolved from elliptical shapes with smaller L/H ratios, reduced posterior regions and shallow gently sloping lunules, to more rounded shapes, with more pronounced anterior and posterior regions and deeper lunules (Text-figs 5A, 6c). Stratigraphical populations had significantly different PC 1 scores

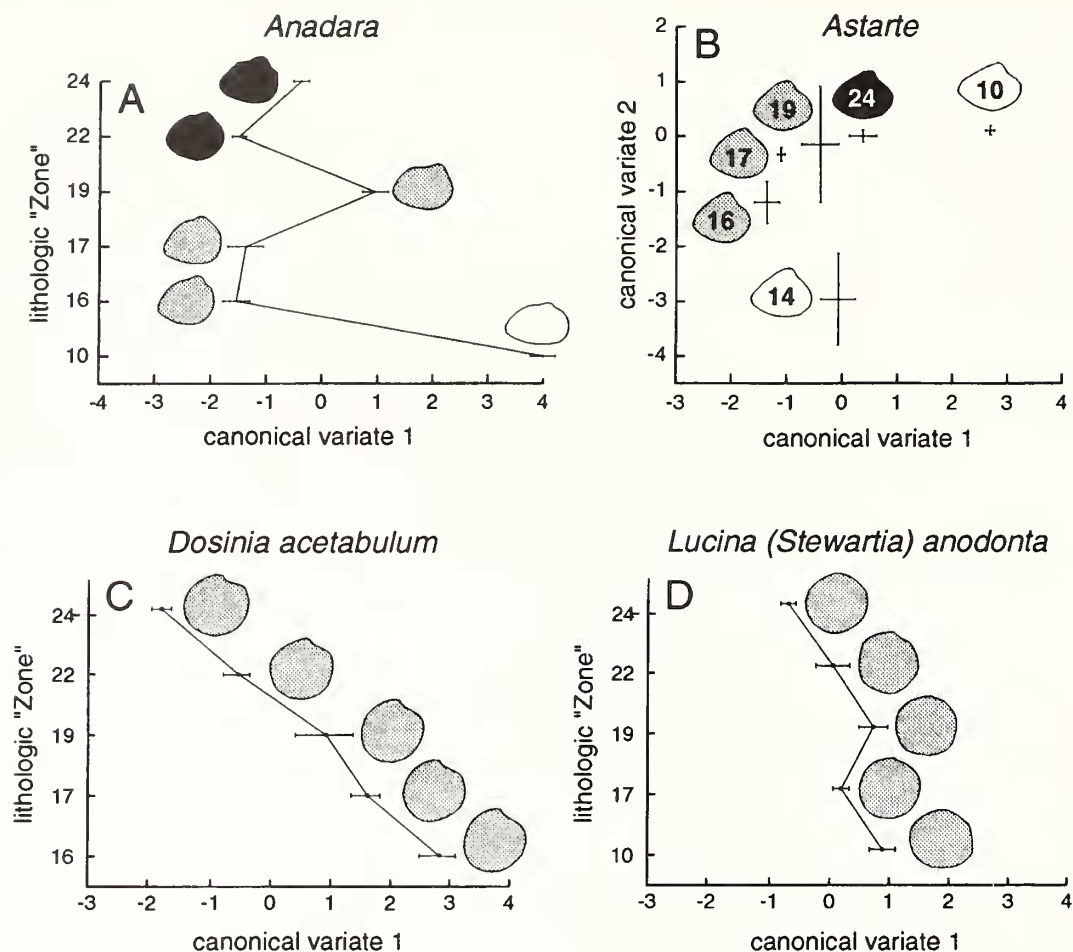


TEXT-FIG. 5. PC 1 score frequency histograms labelled with means and reconstructed end member shapes; C, vertical axis denotes number of individuals which also applies to A and B.

according to Kruskal–Wallis one-way analysis by ranks (Table 3) and the canonical variate 1 monotonic trend was significant according to Spearman's rank correlation analysis (Table 5). Multiple range analysis placed all of the stratigraphical populations into separate groups with the exception of populations from 'zones' 17 and 19, representing a time span of less than 2 million years (Text-fig. 3).

PC 1, accounting for greatest shape variation (Table 2), contributed the most to the canonical variate 1 function (Table 6) and canonical variate 1 accounted for the greatest dispersion between stratigraphical populations (Table 5). Thus temporal shape change made the biggest contribution to total shape variation (Table 6).

Discriminant analysis successfully classified a majority of individuals with their correct stratigraphical level while misclassified specimens were placed predominantly into 'zones' sampled closest to the correct 'zone' (Table 4). The close morphological affinity between adjacent fossiliferous 'zones' suggests that the change from one 'zone' to the next was gradual.



TEXT-FIG. 6. Average canonical variate scores with standard deviation bars and the shape of individuals with scores most closely approximating group centroids; A, white shell is *Anadara subrostrata*, grey shells are *A. staminea* and black shells are *A. idonea*; B, *Astarte* outlines labelled with corresponding 'zones'; white shells are *A. cuneiformis*, grey shells are *A. thisphila* and black shell is *A. perplana*.

Lucina (Stewartia) anodonta Say

No trend is apparent in the PC 1 frequency histograms of stratigraphical populations (Text-fig. 5B). Results of Kruskal-Wallis one-way analysis by ranks revealed that there was less difference between stratigraphical populations of *Lucina (Stewartia) anodonta* than in the other genera studied (Table 3).

Discriminant analysis produced only one canonical variate function and PC 2 was the only PC contributing to canonical variate 1 (Table 6). As PC 2 accounts for only 26 per cent. of total shape variation the discrimination between morphologies of stratigraphical populations is based upon only a quarter of total shape variation; thus three-quarters of shape variation is influenced by factors other than temporal change (Table 2).

Discriminant analysis successfully classified less than 50 per cent. of individuals to their appropriate stratigraphical level, with a larger percentage of incorrectly classified individuals being placed in stratigraphically distant 'zones' versus proximal 'zones' (Table 4). There is no obvious trend apparent in the plot of canonical variate 1 group centroids other than species from 'zone' 24

TABLE 3. Results of Kruskal–Wallis one-way analysis by ranks using PC 1 scores of stratigraphical populations of congeners.

	'Zones'	Ranks		'Zones'	Ranks
<i>Anadara</i>	10	19.46	<i>Dosinia</i>	16	15.10
	16	211.88		17	26.84
	17	184.94		19	35.08
	19	79.15		22	61.80
	22	185.48		24	94.63
	24	138.39	Test statistic = 76.29		
Test statistic = 153.46			Signif. level = 1.11E-15		
Signif. level = 0					
<i>Astarte</i>	10	27.81	<i>Lucina</i>	10	82.82
	14	67.00		17	73.70
	16	101.36		19	56.79
	17	97.74		22	77.00
	19	77.33		24	94.63
	24	66.17	Test statistic = 9.20		
Test statistic = 82.92			Signif. level = 0.06		
Signif. level = 2.22E-16					

TABLE 4. Success of discriminant analysis in classifying individuals to corresponding 'zones'.

Genus	% Classified with correct species	% Specimens classified in		
		Correct 'Zone'	Nearest 'Zone'	Other 'Zone'
<i>Anadara</i> lineage	86.9	66.9	17.5	15.6
<i>A. subrostrata</i>	94.3	94.3	0.0	5.7
<i>A. staminea</i>	80.6	61.1	13.9	25.0
<i>A. idonea</i>	85.9	63.4	23.1	13.5
<i>Astarte</i> lineage	74.7	65.4	16.4	18.2
<i>A. cuneiformis</i>	79.2	79.2	2.0	18.8
<i>A. thisphila</i>	97.9	63.8	34.1	2.1
<i>A. perplana</i>	46.9	46.9	12.5	40.6
<i>Dosinia acetabulum</i>		69.5	26.6	3.9
<i>Lucina</i> (<i>Stewartia</i>) <i>anodonta</i>		42.8	21.7	35.5

are more rounded than earlier species (Text-fig. 6D). The apparent stasis is verified by Spearman's rank correlation analysis which found no significant monotonic trend (Table 5). Multiple range analysis grouped distant stratigraphical populations together, revealing that there was no significant change over more than 9 million years other than the differentiation of 'zone' 24 from earlier stratigraphical populations (Text-fig. 3).

The Astarte lineage

PC 1 accounted for 53 per cent. of total shape variation within the *Astarte* lineage (Table 2). PC 1 frequency histograms reveal that valves evolved from cuneiform to trigonal and then back towards more cuneiform shapes (Text-fig. 5C). Temporal morphological change was significant according to

TABLE 5. Results of non-parametric rank correlation analysis using group centroids for each canonical variate; monotonic trends significant at the 95 per cent. level ($P \leq 0.05$) are denoted by an asterisk.

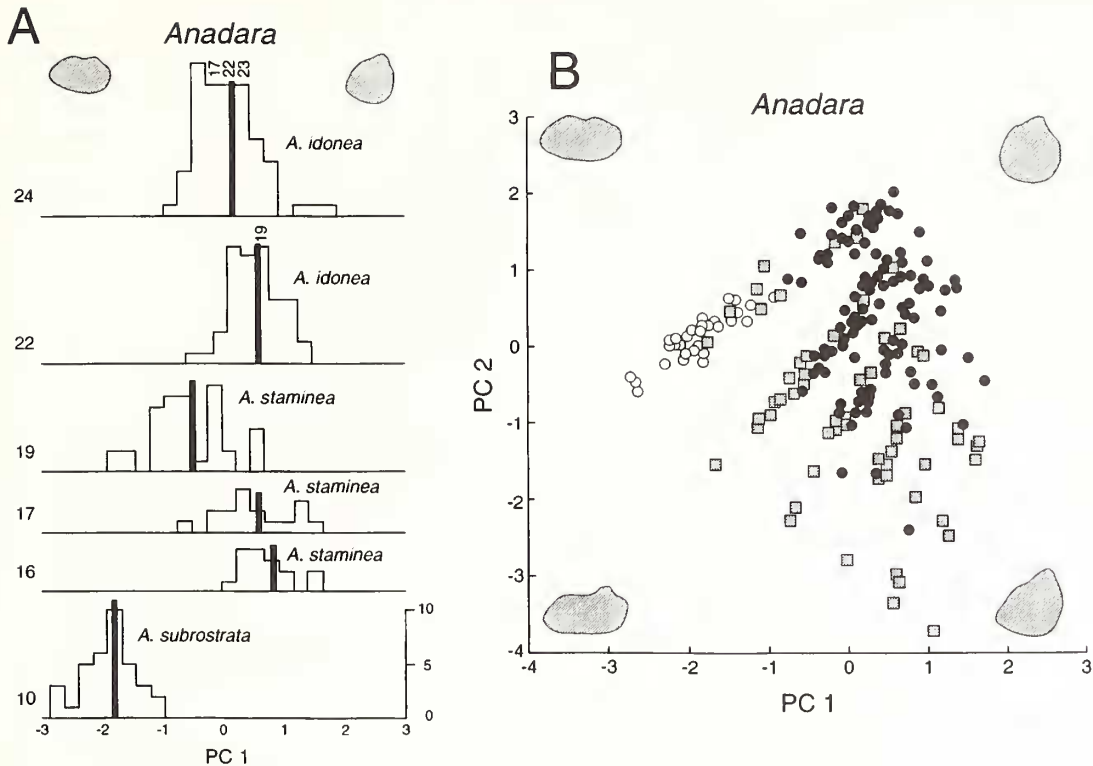
Genus	Canonical variate	% Variation accounted for	Spearman's C	Significance
<i>Anadara</i>	1	71	-0.14	$P = 0.75$
	2	21	-0.09	$P > 0.75$
	3	4	-0.77	$P > 0.075$
	4	2	-0.64	$P > 0.1$
<i>Astarte</i>	1	86	-0.20	$P > 0.5$
	2	8	0.14	$P = 0.75$
	3	5	0.49	$P > 0.25$
	4*	1	-0.89	$P < 0.05$
<i>Dosinia</i>	1*	80	-1.00	$P = 0.00$
	2	17	0.00	$P = 1.00$
	3	2	-0.20	$P < 0.75$
	4	1	0.10	$P > 0.75$
<i>Lucina</i>	1	100	-0.90	$P > 0.05$

TABLE 6. PC coefficients for discriminant functions; canonical variates with significant monotonic trends are marked with an asterisk.

Genus	Axis	PC						
		1	2	3	4	5	6	7
<i>Anadara</i>	1	-2.10	-0.28	0.13	-0.13	0.28	-0.22	
	2	-0.04	0.93	-0.47	-0.71	-0.10	-0.64	
	3	0.02	0.07	-0.06	0.38	0.92	-0.42	
	4	0.13	-0.62	-0.10	-0.77	0.34	-0.04	
<i>Astarte</i>	1	-1.85	-0.35	-0.48		-0.09		
	2	0.17	-0.40	-0.19		-1.00		
	3	-0.02	0.87	-0.54		-0.25		
	4*	0.26	-0.39	-0.80		0.36		
<i>Dosinia</i>	1*	-1.71	0.35		0.38			0.39
	2	0.04	-0.44		1.03			-0.45
	3	0.03	-0.71		0.03			0.74
	4	0.34	0.58		0.47			0.53
<i>Lucina</i>	1		-1.51					

Kruskal-Wallis one-way analysis by ranks (Table 3). The morphological transformation of the youngest species into a shape similar to that of the oldest species was apparent in plots of homogeneous group ranks (Text-fig. 3) and the canonical variate 1 and 2 group centroids of stratigraphical populations (Text-fig. 6B).

Discriminant analysis classified a majority of individuals with their correct 'zones' (Table 4). Discriminant analysis successfully classified 97.9 per cent. of individuals to the *A. thisphila* species while only 46.9 and 79.2 per cent. of individuals were correctly placed into the *A. perplana* and



TEXT-FIG. 7. *Anadara*. A, PC 1 score frequency histograms labelled with means and reconstructed end member shapes; vertical axis denotes number of individuals. B, Plot of PC 1 and 2 scores with reconstructed end member shapes; open circles are *A. subrostrata*, grey squares are *A. staminea* and black circles are *A. idonea*.

A. cuneiformis species, respectively. More incorrectly classified individuals of *A. perplana* and *A. cuneiformis* were placed into stratigraphically distant 'zones' versus levels sampled nearest the correct 'zone'. Mixing of distant stratigraphical populations was due to the transformation of the lineage towards older morphologies. The resemblance between *A. perplana* and *A. cuneiformis* shape was demonstrated by a large percentage of the misclassified individuals being placed in stratigraphical 'zones' corresponding with the other species. The middle species, *A. thisphila*, had a larger percentage of misclassified individuals placed into 'zones' sampled nearest the correct 'zone' suggesting that transformation from the youngest stratigraphical population of *A. cuneiformis*, through all stratigraphical populations of *A. thisphila*, to the single stratigraphical population of *A. perplana* was characterized by mixing of intermediate forms. The presence of intermediate morphologies was further demonstrated with multiple range analysis, which placed the youngest stratigraphical populations of *A. cuneiformis* and *A. thisphila* into two ranks instead of one (Text-fig. 3). Furthermore, PC 1 and canonical variate 1 trends were preserved in succeeding species transformations, which is not inconsistent gradual change. However, it can be argued that the transformation of two homogeneous populations of *A. thisphila* into one population of *A. perplana* resulted from migration of an allopatric *A. thisphila* population into the study area followed by the removal of the earlier population (Text-fig. 3).

Canonical variate 4 had the only significant monotonic trend (Table 5). Canonical variate 4 was most highly influenced by PC 3 (Table 6) having a loading which defined a triangular component of shape (Glassburn 1987, p. 139). The negative Spearman's rank correlation coefficient (Table 5)

indicates that older species have higher canonical variate 4 mean scores and thus, shapes generated by more negative PC 3 scores (because PC 3 has a large negative coefficient in the canonical variate 4 function; Table 6). As more cuneiform shapes would be generated with more negative *Astarte* PC 3 scores (Glassburn 1987, p. 139), the monotonic trend detected by rank correlation analysis of canonical variate 4 was from cuneiform shapes in older species to trigonal shapes in younger species.

The PC which accounted for a majority of total shape variation (PC 1) made the greatest contribution to canonical variate 1, which accounted for 86 per cent. of variation between stratigraphical populations, indicating that temporal shape change had a major influence on overall shape variation. In contrast, canonical variate 4 which accounted for 1 per cent. of variation between stratigraphical populations was influenced predominantly by PC 3 accounting for just 12 per cent. of total shape variation. Thus, the most significant shape trend was from cuneiform to trigonal back to cuneiform shapes. However, there was a small, monotonic trend from cuneiform towards trigonal morphologies.

The Anadara lineage

PC 1 accounted for 53 per cent. of shape variation in the *Anadara* lineage (Table 2). PC 1 frequency histograms showed a dichotomy between inter- and intraspecific shape trends (Text-fig. 7A). Whilst intraspecific trends were from valve shapes with smaller to larger L/H ratios, interspecific trends, which determined the ultimate shape transformation, were from valve shapes with larger to smaller L/H ratios. Temporal shape change was significant according to Kruskal–Wallis one-way analysis by ranks, with the test statistic being nearly double that of the *Astarte* lineage (Table 3).

The plot of PC 1 and 2 scores of the congeners of *Anadara* revealed the presence of at least five different morphological groups (Text-fig. 7B). The odd PC 1 and 2 score pattern was generated with no rotation of the PC loadings matrix. When one of five different rotation methods available in the PC program BMDP4M (Frane *et al.* 1985) was used the pattern was not observed. Thus the appearance of the PC 1 and 2 score pattern may be an artefact of the PC analysis technique. The evolution of all of the *Anadara* morphological groups was from negative PC 1 and 2 scores, generating elongate valves with straight ventral margins to positive PC 1 and 2 scores, generating rounder valves with smaller L/H ratios and curved ventral margins.

Schoonover (1941) noted the presence of different morphological groups of *A. staminea* from different beds at the same locality and between different localities. She observed that variations in shell diameter resulted in variations in valve morphology where specimens with larger diameters had sharper angles at the junction of the anterior and dorsal, dorsal and posterior, and posterior and ventral margins whilst specimens with smaller diameters had outlines less squarely compressed anteriorly and posteriorly. Both Glenn (1904) and Sheldon (1916) noted that some of the variations of *A. staminea* were so distinctive that they had been incorrectly described as separate species. Therefore a preliminary study of geological factors which may have contributed to the presence of the different morphological groups was conducted. When the individual points were labelled according to valve area it was revealed that size did not contribute to the PC 1 and 2 pattern and thus the different morphological groups were not the result of ontogeny (Glassburn 1987, figs 8.37–8.40). Also, the five morphological groups do not represent geographical populations; for instance there were five morphological groups of *A. staminea* from 'zone' 19 sampled at two locations (Calvert Cliffs State Park and Camp Baybreeze; Glassburn 1987, fig. 8.40). Furthermore, the morphological group containing individuals of *A. subrostrata*, *A. staminea* and *A. idonea* had individuals sampled from localities spanning the entire length of the study area from Randle Cliffs Beach to Chancellor's Point (Text-figs 2, 7B). This study cannot clarify whether or not the morphological groups are ecophenotypes, as they might have resulted from differences in local palaeoecology. A more extensive field investigation is required before the PC 1 and 2 pattern can be dismissed as merely an artefact of the shape technique.

Discriminant analysis placed 67.2 per cent. of individuals into the correct stratigraphical level, but was much more successful classifying individuals according to species (Table 4). Thus, there was a

greater distinction between the morphology of species than stratigraphical populations. More incorrectly classified individuals were placed into stratigraphically proximal 'zones' rather than distant 'zones'. However, mixing between proximally sampled stratigraphical populations was predominantly within species with only 2 per cent. of the misclassified individuals being the result of mixing between the youngest population of an ancestor species and the oldest population of its descendant.

Non-parametric rank correlation analyses of canonical variate group centroids revealed no significant monotonic trends (Table 5). Plots of canonical variate 1 group centroids and canonical variate 1 and 2 homogeneous rankings revealed that the direction of species' trends was not preserved with subsequent speciation (Text-figs 3, 6A). Furthermore, a greater amount of change occurred with speciation than with any intraspecific change. The canonical variate 1 plot revealed that overall morphological transformation of the lineage was from species with larger L/H ratios to valves with roughly equivalent lengths and heights. Canonical variate 1, which accounted for 71 per cent. of variation between stratigraphical populations, was most highly influenced by PC 1, which accounted for a majority of total shape variation; thus, variation between stratigraphical populations made the biggest contribution to total shape variation. However, speciation contributed the most to temporal variation.

Comparison with earlier morphometric studies of the Maryland species

The observed lack of congruent temporal patterns between Chesapeake Group bivalves was also noted by Kelley (1984). The morphological variation was probably not the result of shared ecophenotypic responses but the result of genetic variation.

In common with the present study, Kelley (1983a, 1983b, 1984) observed that the *Anadara* lineage had an evolutionary tempo consistent with punctuated equilibrium. The present study found that overall morphological transformation of the lineage was determined by interspecific trends which were from elongate shapes, with straight ventral margins, to rounder shapes, with curved ventral margins. Stanley (1970) describes two life modes for extant *Anadara* species: (1) an infaunal or epifaunal byssally attached life mode which preceded the development of (2) free burrowing forms. Species with byssally attached life modes, such as *Anadara antiquata*, are distinguished from free burrowers, such as *A. ovalis* and *A. chemnitzii*, by their more elongate shapes, where an elongate and flattened ventral margin provides a broader means of support for byssal attachment (Stanley 1970). The *Anadara* lineage in this study was composed of elongate forms, especially *A. subrostrata*, suggesting a byssally attached life mode. The supposition that the *Anadara* species in this study were byssally attached is supported by Gernant (1970), who described the *Anadara* species as semi-infaunal suspension feeders. The general transformation of the *Anadara* lineage was from forms more ideally suited to a byssally attached life mode towards shapes more reminiscent of burrowing forms.

As in this study, convergence between youngest and oldest *Astarte* species' morphologies was observed by Kelley (1983a) in seven out of eight measured characters and Schoonover (1941), who noted that *A. perplana* resembled some of the Randle Cliffs Beach *A. cuneiformis* specimens (Text-figs 5C, 6B). Furthermore, Schoonover (1941) observed that *A. perplana* had a smaller L/H ratio, being more trigonal in shape than *A. cuneiformis*, which supports the results of rank correlation analysis which revealed a monotonic trend in canonical variate 4 centroids from cuneiform valve shapes towards more trigonal forms (Table 5). In contrast to the present study, Kelley (1983a, 1983b, 1984) reported an evolutionary tempo of punctuated equilibrium within the *Astarte* lineage. However, morphological intermediates between *Astarte* species were observed by Schoonover (1941) and Kelley (1983a) consistent with gradual change having occurred.

In contrast to this study, Kelley (1983a) observed stasis within *Dosinia acetabulum* (Conrad). Disparities in evolutionary tempos observed between this study and Kelley's (1983a, 1983b, 1984) studies of the *Astarte* lineage and *Dosinia acetabulum* may have been due to differences in the

evolution of valve shape versus biometric parameters measured by Kelley (1983a, 1983b, 1984). Probably, more significant is the difference in the temporal resolution of the two investigators' studies. As results in this study were based upon specimens collected from fewer stratigraphical levels, apparent gradual trends may have resulted from consistent direction in punctuation events or sampling of a zigzagging stasis trend coincidentally resembling unidirectional change.

In contrast to this study, Stanley and Yang (1987) found that stasis best described the evolutionary mode of *Dosinia acetabulum*. Their results were based upon calculations of the area of non-overlap of two populations' first eigenshapes as a percentage of the area of fossil eigenshape. However, discriminant analysis based on twenty-four morphometric variables, including aspects of valve shape, revealed some monotonic trends in *D. acetabulum* (Stanley and Yang 1987, fig. 17).

Stanley and Yang (1987) state that *D. discus*, a US East Coast extant species, arose from *D. acetabulum*. *D. discus* is a rapid burrower preferring sandy substrates and has disc-shaped valves which it uses to slice vertically downward into the substrate (Stanley 1970). While this study reports that *D. acetabulum* valves gradually evolved from oblong to disc-shapes (Test-figs 4A, 5C), Stanley and Yang (1987) found that temporal shape variation in *D. acetabulum* was minor relative to geographical variation and that interspecific change within the 'lineage' containing *D. acetabulum* and *D. discus* was characterized by a speciation event or rapid phyletic change. The present study requires sampling from a wider geographical area and comparison between intra- and interspecific variation within the corresponding 'lineage' of *D. acetabulum* in order to support conclusions concerning evolutionary mode. The monotonic trend observed by the present study may be a minor trend in a larger time frame of zigzagging morphological stasis, or a bend in an anastomosing stream of change in which geographical variability was as great as temporal variability.

Like the present study, Kelley (1984) found that stasis best described temporal shape variation in *Lucina* (*Stewartia*) *anodonta* Say. Only individuals of *L. anodonta* from 'zone' 24 could be distinguished from other stratigraphical populations, being smaller and more inflated than the earlier specimens (Schoonover 1941; Kelley 1984). Stasis in *L. anodonta* is supported by the species persistence from the Miocene to the Recent (Bretsky 1976).

DISCUSSION

There were many similarities in results using the PC shape technique and previous studies which used other morphometric techniques to describe temporal shape change within the same bivalve species. Furthermore, many aspects of temporal shape variation highlighted by the PC shape technique were also reported in a thorough study by Schoonover (1941) who made qualitative observations about temporal morphological changes. Although there were some discrepancies between evolutionary tempos and modes reported in this and previous studies the cause was most probably the difference in temporal resolution, where this study sampled from fewer stratigraphical horizons or from a more limited time span and geographical range. Limitations in the sampling scheme notwithstanding the PC shape analysis technique proved to be a fast and simple way to characterize fossil outline shape. Its strength over qualitative assessment of temporal shape change is that it quantifies shape, providing a more objective way to compare shapes of different stratigraphical populations. The advantage of using PC shape analysis versus point-to-point measurement techniques, as with all image analysis techniques, is the speed at which morphological information can be collected.

One doubt concerning the validity of morphometric techniques which process outlines is that comparisons are made between non-homologous points whereas techniques utilizing point-to-point measurements can target homologous points (Bookstein *et al.* 1982; Full and Ehrlich 1986). There are generally few homologous points present on the peripheries of simple invertebrates and outline processing techniques which compare points connected by equiangular radial lengths (e.g. Fourier and PC shape analysis) or equal chord lengths (e.g. Eigenshape analysis) can only be certain of achieving correspondence with respect to one homologous point if it is the initial point.

Although PC shape analysis performed calculations between non-homologous points, the first two PC loadings, accounting for greatest shape variation, were always orientated in relation to morphological landmarks (Text-fig. 4A). PC 1 loadings always contained two pairs of lobes with axes 90° to each other. One axis always connected the umbo with the ventral margin (defining shell height) and the other axis defined shell length. PC 2 loadings always contained two pairs of lobes orientated 45° to the lobes of the PC 1 loadings, with one axis connecting the lunule with the point of intersection between the posterior and ventral regions and the other axis connecting the point of intersection between the posterior and dorsal regions with the point of intersection between the anterior and ventral regions.

Possibly more important than recording changes between limited homologous points present on a bivalve periphery is recording distortions in bivalve shape occurring to accommodate changes in shape or size of soft body parts. An interesting project for the future would be to use PC shape analysis to describe bivalve shape and the shape of muscle scars in order to determine how changes in the shape of the muscle attachment area impacts upon valve shape.

SUMMARY

1. Cubic interpolation reduced 100–200 x – y coordinates of a properly rotated valve periphery to thirty-six radial lengths spaced at equiangular intervals. The thirty-six radial lengths were then used as variables in principal components analysis reducing the original data set to less than eight principal components accounting for approximately 90 per cent. of total shape variation (Table 2). PC scores were used as shape variables in discriminant analysis and non-parametric rank correlation analysis to determine whether significant intra- and interspecific shape trends existed.

2. Original shape was reconstructed by destandardizing results of matrix multiplication of PC scores with PC loadings (Text-fig. 4).

3. Phyletic gradualism was implied in a lineage where the direction of an intraspecific shape trend was retained with the transformation of that species into the next species and total shape change was equally influenced by intra- and interspecific trends.

4. Punctuated equilibrium was implied in a lineage where interspecific trend directions varied markedly from associated intraspecific trends and intraspecific temporal variation contributed much less than speciation to total shape change.

5. Discriminant analysis demonstrated that a species population in one stratigraphical level was measurably different in shape from a population in another stratigraphical level. If a high percentage of misassigned individuals were placed in proximal stratigraphical levels it indicated a mixing of morphological intermediates implying a gradual change.

6. The valves of *Dosinia acetabulum* (Conrad) evolved gradually from oblong to disc shapes (Text-figs 5A, 6C).

7. Stasis best described the temporal shape trend of *Lucina* (*Stewartia*) *anodonta* Say (Text-figs 5B, 6D).

8. The *Astarte* lineage evolved gradually from cuneiform to trigonal and back to wedge shapes (Text-figs 5C, 6B).

9. The *Anadara* lineage exhibited an evolutionary mode consistent with punctuated equilibrium. Intraspecific trends were from valves with smaller L/H ratios to more elongate shapes, whilst interspecific changes, controlling ultimate shape transformation in the lineage, were from elongate valves with straight ventral margins to valves with smaller L/H ratios and curved ventral margins (Text-figs 6A, 7).

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